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IS THE BOX ELDER A MAPLE?

A STUDY OF THE COMPARATIVE ANATOMY OF NEGUNDO

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(WITH PLATES V–X)

The difficulties and uncertainties of classification, upon the basis of purely superficial characters, is perhaps nowhere better exemplified than in the case of the common box elder.

This tree occurs in large numbers over the greater part of its range throughout the northern portion of the United States and Canada, and only less frequently in the Southwest and along the Pacific Coast. It is also very generally cultivated in Europe.

With its diffuse, irregular mode of branching, and its light green, compound leaves, the box elder is one of our most easily identified trees, yet it possesses combinations of characteristics that constitute a troublesome puzzle to the systematist.

The tree habit is manifestly quite different from that of the true maples; the leaves are wholly unlike maple leaves; the sap is similar to that of maples, but the odor of the young twigs is unlike anything ever produced by a maple; the fruit is quite like the maple fruit; yet, unlike the maple, the box elder is anemophilous and strictly dioecious; the wood is maple-like in appearance and structure, though much softer, lighter, and less durable.

These and many other peculiarities of the box elder have engaged the attention of botanists since LINNAEUS named this tree *Acer Negundo* in 1753. To the mind of LINNAEUS, even approximate agreement in reproductive structures and processes easily outweighed in importance the most conspicuous differences in general morphology. In 1794 MOENCHHAUSEN set up for the box elder the new genus *Negundo*, at the same time recognizing the close relationship to *Acer* in the name *Negundo aceroides*. Extreme opposition to the Linnaean rating of the box elder was developed by KARSTEN, who in 1880 gave the name *Negundo Negundo*. Each of these three names is held in favor by a considerable group of botanists at the present time, though KARSTEN has a much smaller following in this matter than either LINNAEUS or MOENCHHAUSEN.

To all three of these men, as well as to most of their followers, the minute anatomy of plants was of course a sealed book, whose importance was wholly ignored because unknown and unsuspected. It remained for DE BARY, VAN TIEGHEM, and a host of more recent investigators, to discover and demonstrate the fundamental significance and value of anatomical features in the study of phyletic relationships.

The following study of the comparative anatomy of the box elder was undertaken a few years ago, in the hope that some additional light might be thrown upon the problem involved in the title of this paper.

General morphology

As is well known, the box elder is usually a rather low-growing, irregularly and diffusely branching tree, hardly more than a shrub in many parts of its range, attaining to its maximum size of 50–70 feet in height, with a trunk diameter of 2–4 feet, only in the lower Ohio Valley. In a number of characters the box elders show a remarkable range of variety.

Referring to fig. 1, it appears that the compound leaves are 3–9-foliolate, with the leaflets variously toothed, lobed, and divided. The range in leaf types is apparently not so great in the eastern part of North America as it is in the central part. Most of the descriptive works published in America follow the early writers in stating that the leaves are 3–5-foliolate. As the result of a careful statistical study of 1250 box elder trees in southeastern Wisconsin, it was found that the leaves were predominantly of the 3-foliolate type on a little more than 5 per cent of the trees; 5-foliolate leaves were in the majority on more than 32 per cent; while on about 62 per cent of the trees most of the leaves were 7-foliolate. Two trees out of the entire number showed 9-foliolate leaves in greatest numbers. No tree bore one type of leaf exclusively, except a very few having only the 3-foliolate sort. No 3-foliolate leaves occurred on the 7 and 9-foliolate trees, neither did the 9-foliolate leaves appear on 3 and 5-foliolate trees. The higher number of leaflets, as well as the larger and more deeply lobed leaves, occur on suckers and second growths. In general, the leaflets are more numerous, larger, and more deeply divided on staminate trees. The two 9-foliolate trees mentioned above were both staminate trees.

More than 7 per cent of the leaves studied bore trifoliololate basal leaflets, such as are shown in no. 6 of fig. 1. Intermediate forms appear in nos. 3, 4, 5, and 7 of the same figure. It was impossible to detect any intimate and constant relationship between leaf types and the quality of the soil in which the trees grew. Light and shade relations seem to be more effective agents in this respect, the higher number of leaflets usually occurring on the more brightly lighted trees and parts of trees. The leaves of box elder are commonly thicker and of softer texture than are those of true maples growing in similar situations.

An interesting peculiarity of the box elder is its very common habit of developing new buds and leaves as long as the growing season lasts. In other words, its growth is indeterminate. This characteristic seems to be more pronounced in the northern part of the range. Here not uncommonly the box elder trees continue to develop new leaves at the tips of the twigs until checked by the first killing frost. This fact accounts for the diffuse and angular habit of the trees in the colder parts of the range, since because of this mode of growth the terminal buds are usually killed, and the lateral buds carry on the development in the following season. Indeterminate growth is much more conspicuous in the male trees than in the female, especially in those years when the female trees bear a heavy crop of fruit. This in turn explains why the female trees are so much more symmetrical in form, and hence better suited for artificial planting and cultivation, than are the male trees.

In a series of forcing experiments, twigs of box elder and of several species of maples were placed in the hothouse at intervals throughout the winter. All were subjected to uniformly favorable conditions for development. The box elder buds opened in about one-half the time required by the maples. The same quick response is noticeable in the box elder in the first warm days of early spring. By thus utilizing the maximum length of the growing season, the box elder is able to make its remarkably rapid growth. This again is particularly true of the male trees.

Brilliant autumnal colors are not developed by box elder leaves. Toward the close of long or dry growing seasons, all but the very young leaves turn a dull greenish yellow, but do not fall in any considerable numbers until after frost, when the trees may be entirely stripped in a single day. In many of the characteristics here noted, the leaves of the box elder differ strikingly from those of the true maples.

The young twigs of box elder also show marked differences. Two types are commonly described. In one of these types the twigs are of a pale grayish green color, usually quite slender, and with rather short internodes. In the other type the twigs are of a maroon color, often covered with a white bloom, stout, and with longer internodes. These two forms are said to occur in almost equal numbers in the eastern part of the range, while the green type predominates in the southern part, and the maroon type in the northern part. In the course of these studies, it has been found that green twigs are usually developed by female trees, and maroon twigs on male trees. However, the color of the twigs, in addition to being in a measure a secondary sex character, is subject largely to weather conditions, exposure, etc. Thus we find vigorous young shoots of both sexes pale grayish green in color when growing in protected or poorly lighted situations, while both take on more or less of the maroon tint when exposed to full light and severe weather conditions. Also it is to be noted that the maroon color in all these twigs gives place more or less completely to green in the warm days of spring. In all probability we have here to do with a phenomenon similar to the development of rhodophyll and anthocyanin in autumn leaves, in rosette plants in winter, in alpine types, etc.

In the series of hothouse experiments already mentioned, it was observed that all lateral buds in the box elder are of nearly equal vitality, and that most of them spring into active development at the first favorable opportunity. It was also observed that the box elder twigs were able to develop a much greater amount of new growth from their stored food material than were true maple twigs or even poplar and willow twigs of the same size. In the matter of rhizogenetic capacity, the twigs of box elder compare well with those of black poplar, and while the development is not so rapid as in the case of willow twigs, the number of roots developed is considerably greater, one or more appearing at every lenticel. Thus the propagation of the box elder by cuttings is comparatively easy, while in the case of true maples it is well-nigh impossible.

On the older trunk surfaces the bark of the box elder shows a very characteristic "expanded metal" appearance, with the rather blunt ridges arranged in a fairly regular oblique diamond pattern, as shown in fig. 2. This is wholly unlike most of the true maples, in which the bark is seldom ridged, but in which it usually scales off in larger or smaller thin plates, as shown in fig. 3. The most notable exception to this rule among maples is *Acer platanoides*, which, by the way, seems to be one of the few contact points between the true maples and the box elder. In fact, the trunk surface of the box elder is strikingly similar to that of the white ash, even to the gray or grayish brown color.

Anatomy of the root

The root system of the box elder is very wide-spreading in comparison with the size of the tree. Slender fibrous roots are developed in immense numbers, forming a close-meshed network to an unusual depth in the soil. Where a larger root is uncovered and exposed to the air and light, buds appear and rapidly develop into vigorous shoots, much as in the case of the adventitious buds that form so abundantly on roots of the common locust, when they are exposed or injured. This bud-forming activity of box elder roots is especially marked when the main trunk has been injured in any way. Thus great clumps of second-growth shoots are likely to spring up around the stumps of recently cut trees.

Fig. 7 shows the more prominent features of the anatomy of a young box elder root. The pith is almost all eliminated by growth pressure. Medullary rays are numerous, straight, 1–2-seriate, and expanded considerably in the inner bark. Tracheae are large and very numerous, often in clusters of 5 disposed in radial rows. Tracheids are large, and of thin-walled and thick-walled sorts disposed in irregular groups in such a way as to give a marbled appearance to the section. The cambial zone in growing roots is 8 or 10 cells thick. The bark is comparatively thin, and contains but very few sclerotic, crystallogenous, or tanniniferous cells. The many large sap-storage cells and canals are a conspicuous feature of the bark. The dead bark scales off in small thin plates, leaving the root quite smooth, in striking contrast to the appearance of the older stems.

A comparison of figs. 6 and 7 makes it evident that the maple root is heavily charged with tannin in the older part, the wood is more compact, the bark is thicker, more dense with numerous groups of stone cells, few sap reservoirs, and it scales off in larger plates. The cambial zone is not so extensive, and everything about the structure points to a less vigorous functional activity in the root of the maple than in the root of the box elder. The appearance of the medullary rays in the outer wood and bark of an older root of *Acer rubrum* is shown in figs. 11 and 12. Fig. 12 also shows fairly well the irregular massing of the sclerotic cells of the bark. Assuming the root to be a very conservative structure, it is interesting to compare this figure with figs. 13–16 inclusive, which show corresponding regions in some stems.

Reference may here again be made to the remarkable rhizogenetic powers of box elder stems when covered with water or buried in moist soil. Young shoots may be propagated by cuttings or by "layering," as in the case of many berry canes.

Anatomy of the stem

The young shoots of box elder are commonly of very robust growth, especially in the male plants, and on all second growths. Not infrequently the season's growth may reach a length of 5 or 6 feet, with a basal diameter of five-eighths of an inch or more. The twigs are not quite cylindrical, but more or less elliptical in section, the longer axis lying in the plane of the two leaves borne at the top of the internode. The surface of the young twigs is quite smooth and shining, except in those forms which develop a whitish bloom. Lenticels are not very numerous, but they are of rather large size, long and narrow in the early part of the season, and later becoming broad.

Fig. 19 shows a section of a moderately vigorous young shoot of a male box elder. For comparison a section of a young stem of *Acer saccharinum* is shown in fig. 17. The characteristic 6-sided appearance of the pith in the box elder section is due to the symmetrical arrangement of the 6 large leaf traces, 3 for each leaf. These leaf traces are of course most prominent near the top of the internode, but they are conspicuous even to the lower end. The section was taken from near the middle of an internode 5 inches long. While the leaf traces are prominent in all types of box elder, it is worthy of note that they are relatively much larger in those plants which bear leaves with the higher numbers of division.

The medulla is usually about one-half the diameter of the stem. The pith cells are large, thick-walled, circular, oval, or hexagonal in outline, and usually quite empty, except in the outer amyliferous zone. Fig. 40 shows a portion of this zone, very greatly magnified. While the zone is very irregular in width, it is everywhere at least 3 or 4 cells wide. In the true maples this starch zone is much narrower, even sometimes entirely absent. An average condition of the starch zone of *Acer saccharinum* is shown in the drawing fig. 41. It will be observed, also, that the medullary ray of box elder is expanded at its inner end, thus affording a better connection with the starch zone than in the case of the maple. The box elder's quick response to the first warmth of spring is doubtless made possible, in part at least, by its large starch-storing capacity and its highly efficient medullary rays. These rays are very numerous, mostly uniseriate, and seldom much farther apart than the width of a large trachea. The cambial zone, in the growing season, is made up of a considerable number of layers of actively dividing cells, thin-walled, and filled with protoplasm. The bark is comparatively thin on young twigs, and is composed of small, thin-walled cells for the greater part of its thickness, with a few layers of collenchyma toward the outside, covered by a small-celled epidermis over which is spread a smooth, uniformly thick cuticle. Sclerenchyma tissue occurs as a narrow and frequently interrupted band of bast fibers, with numerous small and irregularly scattered masses of stone cells. The bark contains some starch, and usually a few large empty cells, corresponding to the sap-storage cells of the root. No true phellem is formed in the first season.

Comparing figs. 19 and 17, it will be seen that the leaf traces of the maple are inconspicuous, the medullary starch zone is not prominent, medullary rays are less numerous, and the bark is thicker and more dense. In twigs of *Acer rubrum* the starch zone is thinner; there is less sclerenchyma; no phellem, but many thick-walled tanniniferous cells; cuticle thick and lenticular over a larger-celled epidermis. In *A. saccharum* and *A. platanoides,* the starch zone is thin; few medullary rays; but little sclerenchyma; phellogen and phellem very prominent, with numerous large lenticels; epidermis early tanniniferous; cuticle thin and smooth.

The medullary rays of box elder are continued far out into the cortex, both in young and in older stems. A study of figs. 13–16, which show sections of older stems, will make clear the relative development of box elder in this respect. Further comparison with figs. 11 and 12 indicates that this prominent development of the medullary rays in the cortex of box elder is a primitive ancestral characteristic, as well as another important factor making for rapid growth.

An additional point of interest in this connection is found in the form and number of the pits in the walls of both the ray cells and the cells of the amyliferous zone. While these pits are comparatively small in the box elder, they are far more numerous here than in any of the true maples. Moreover, they are ideally arranged to facilitate the movement of sap to the regions of most active growth. For comparison of sizes of the various cells, and the thickness of the walls, the reader is referred to table I. In general, it may be said that the tissues of the young stem of box elder are much less compact than in the case of the true maples.

TABLE I

SIZES OF VARIOUS TISSUE ELEMENTS IN SOME SPECIES OF *Acer*, AS SEEN IN CROSS-SECTION

Tissue type	Acer Negundo	A. platanoides	A. rubrum	A. saccharum	A. saccharinum
Medulla cells	40–60 μ diam.	30–60 μ diam.	40–50 μ diam.	20–40 μ diam.	45–55 μ diam.
Wall thickness	0.2–0.3 μ	0.1–0.2 μ	0.3–0.4 μ	0.2–0.3 μ	0.4–0.5 μ
Amyliferous cells	10–15×25–40	8–10×12–25	10–12×15–25	8–12×15–25	10–12×15–30
Wall thickness	1–2 μ	0.7 μ	0.6 μ	1–1.5 μ	0.6–0.7 μ
Tracheae	30–40×55–65	20–30 μ diam.	20–40 μ diam.	10–20×15–30	20–40 μ diam.
Wall thickness	0.6 μ	0.7 μ	0.5–0.6 μ	0.5 μ	0.7–0.8 μ
Tracheids—					
Thin, summer	12–15 μ	7–10 μ	6–15 μ	8–12 μ diam.	8–12 μ diam.
Thick, "	8–10 μ	......	......	7–10 μ diam.	......
Autumn	5–7×10–15	4–8×10–15	3–4×10–14	5×10 μ	4–5×12 μ
Medullary rays, wood	1–3-seriate	1–3-seriate	1–6-seriate	1–3–(5)-seriate	1–3-seriate
Ray cells, t.s.	7–10×25–40	8–12×30–40	8–12×40–75	8–10×35–50	6–10×30–60
Parenchyma, bark	15×35–40 8–10×30–45	...... 8–12×15–17	...... 10–15 μ oval	...... 5–8×10–15	3–4×12–14 10–14×20–25
Ray cells, bark	8–12×25–30	8–12×25–30	10–18×15–25	8–16×25–30	10–18×18–25
Bast fibers	10–12 μ diam.	10–12 μ diam.	10–17 μ diam.	8–10 μ diam.	10–15 μ diam.
Cavity	1–2 μ diam.	1–3 μ diam.	1–5 μ diam.	1–2 μ diam.	0.5–1 μ diam.
Stone cells	25–40 μ diam.	20–30 μ diam.	25–35 μ diam.	25–35 μ diam.	20–35 μ diam.
Crystallogenous	10–18×15–25	15–20×25	12–15×15–20	10–18 μ diam.	12–20 μ diam.
Phellem cells	7–12×20–35	10–15×25–30	5–7×15–17	3–10×18–22	7–8×15–18

Considering now more specifically the minute anatomy of the older trunk of box elder, we find that the rough "expanded metal" appearance of the trunk surface shown in fig. 2 is almost exactly reproduced in the photomicrograph of a tangential section of the bark (fig. 24). The numerous concentric layers of bast fibers are imbedded in a spongy mass of soft, thin-walled parenchymatous phloem, which is split up into thin radial plates by the medullary rays. Near the cambial zone these layers of hard bast are almost continuous, except where perforated by the thin medullary rays. As the sheet of hard bast is forced outward by growth, the fibers cling tenaciously to each other, and the whole sheet is expanded into an oblique diamond-mesh pattern, as a result of the great tangential tension. At the same time, centripetal pressure is brought to bear upon all of the tissues inside the network of bast fibers. As a result of these conditions, there is more or less radial compression and tangential expansion of all the softer elements of the bark. For the same reasons, there is likely to be a considerable tangential shifting of each layer of hard bast with reference to that next inside. When this shifting is all in the same direction in all the layers, the medullary rays are often bent aside 30° or 40° from the radial line. This is of course a common feature in those plants in which the medullary rays extend far out through a thick bark. The hard bast fibers are quite slender, except occasional isolated specimens, but they are usually several millimeters long, and very firmly united with each other. The walls are very thick, often almost eliminating the cell cavity. Angular, irregularly shaped sclerotic cells are found in fairly large numbers, most frequently in the angles of the bast fiber network. In the young bark the medullary ray cells are oval in form, and occur in loose moniliform rows. The nuclei are here of large size and the protoplasm is especially abundant. The medullary ray cells in the outer part of the live bark are shorter and thicker. As seen in tangential section, these cells are commonly drawn out transversely into an oval shape. In the still older bark the ray cells are empty, crushed and distorted by the pressure of growth. The bast parenchyma begins its development in the form of thin-walled, radially compressed cells about the diameter of autumn wood cells. From these are derived two types of parenchymatous cells: the larger are 15 μ×35–40 μ in size, becoming crystallogenous in the older part; the smaller 8–10 μ×30–45 μ in size, and are more numerous, in the ratio of about 3 to 1 of the larger. The walls of the larger are not lignified at any stage, while the walls of the smaller cells are slightly lignified at maturity. Sieve tubes are numerous in the younger bark, with large sieve plates especially conspicuous in tangential sections. The outer, dead bark consists of a mass of crushed, irregular, thin-walled cells, alternating with several zones of thick-walled phellem. Each zone of phellem is made up of 3–8 layers of brick-shaped cells, 7–12 μ thick radially, and 20–35 μ square on the tangential surface. These cells are very thick-walled (2–4 μ), lignified, and only the outer ones in each zone are conspicuously suberized. Progressive parenchymatous degeneration of the hard bast and stone cells occurs in the outer portion of the live bark, so that very few of these elements are to be found in the dead bark of the box elder.

In the radial section of box elder bark (fig. 25) the bast fibers appear apparently in discontinuous masses, scattered throughout the live portion of the bark. As a matter of fact these strands are connected longitudinally for great distances, but, owing to the fact that they are tangentially oblique, the section shows only short portions of each strand. This type of structure evidently gives great strength to the bark, while at the same time it secures a maximum degree of elasticity even where the bark is quite thick, thus readily permitting the rapid expansion so characteristic of the growing box elder stem.

In the case of *A. saccharinum*, the bark is thinner than in box elder, and quite smooth even in older trunks, scaling off from larger trunks in thin, even plates (fig. 3). Under the microscope, the cross-section of a 10-year twig shows the bark to be made up of parenchyma in alternating narrow zones of radially compressed cells and round cells, with 2 or 3 nearly continuous zones of hard bast lying close together near the middle of the bark, and also many small scattered islands of sclerotic cells, both inside and outside of the bast fiber zones.

The medullary rays are commonly bent aside from the radial line 20–30°, to the first hard bast zone, where they are again nearly radial, but beyond which they quickly disappear.

In radial and tangential views the most striking feature is the incoherence of the hard bast zones. Only rarely do the elements hold together in a diamond-mesh network, such as is so characteristic of the box elder. This is apparently due to the fact that most of the hard bast cells are comparatively short, blunt at the ends, and not interlocked to any great extent. In the outer part of the bark some of the fibers lie in the tangential plane almost at right angles to the axis of the stem, as the result of the great tangential tension in this region. There is extensive parenchymatous atrophy of the sclerotic elements in the outer bark. Only one phellem zone is commonly present. This is made up of 6–10 layers of small cells, quite thin-walled and strongly suberized. Crystallogenous cells are found in small numbers, principally in the middle and outer portions of the bark. Occasionally an older medullary ray cell is found containing tannin.

In *A. rubrum* (fig. 16) the bark is much thinner than in box elder, smooth on young stems, and separating into thin regular plates on older trunks. Hard bast occurs in larger proportion than in *A. saccharinum*, and is distributed quite irregularly throughout the outer three-fourths of the thickness of the bark. The zonation is imperfect, and there is scarcely any tendency to form a diamond-mesh network (fig. 23).

Only the larger medullary rays extend out into the bark. These are only slightly oblique as far as the first hard bast, beyond which they extend radially one-half to two-thirds of the way to the outer surface, becoming increasingly diffuse. Crystallogenous cells are quite numerous, while tanniniferous cells occur less frequently. The parenchyma cells are nearly all much flattened. The hard bast zones and masses are incoherent and the cells are drawn out to oblique and transverse positions in the outer bark. There is a single zone of phellem, 5–12 cells thick, the walls strongly lignified and suberized.

The bark of *A. saccharinum* (fig. 15) is thin, and shows a definite zonation of hard bast in the inner two-thirds of its thickness. The zones are 2 or 3 cells thick, interrupted by the broad medullary rays which usually disappear about half-way out through the bark, beyond which point the sclerotic tissue is very irregularly scattered and progressively atrophied. Most of the parenchyma cells are irregularly flattened. Both tanniniferous and crystallogenous cells are collenchymatous. The single phellem zone is 5–10 layers of cells thick, suberized, but only slightly lignified. Sieve plates are prominent in tangential view of the youngest phloem.

A. platanoides (fig. 14) shows a much smaller proportion of hard bast than do most of the other maples. There are only 2–4 narrow zones, and these are widely interrupted by the broad, irregular medullary rays, which extend about two-thirds of the way to the outer surface of the bark. The rays are not much deflected from a radial course, and the deflection is not at all uniform. The parenchyma is less flattened than in other forms. The bast fiber network is least coherent in this species. Crystallogenous and tanniniferous cells are very numerous. Parenchymatous atrophy is pronounced in the outer part. There is a single zone of phellem, very irregular in thickness. The cells are highly suberized. The collenchyma zone just inside of the phellem is conspicuous and of uniform width around the stem.

These brief studies of box elder and of four species of maples, together with the measurements of elements tabulated on p. 177, show that the bark of the maples is more dense and better able to resist unfavorable conditions and the attack of enemies, but less rapid in growth, less elastic, and hence less perfectly adapted to the needs of a quick-growing tree than is the bark of the box elder.

In figs. 26, 27, and 28 are shown sections in three planes of the wood of *A. saccharinum*, while the three succeeding figures show corresponding sections of box elder wood. The maple wood is evidently more compact, with somewhat smaller elements arranged with greater regularity than in the case of box elder, thus readily accounting for the fact that the maple wood splits more easily than the box elder wood. The groups of tracheae are larger in the box elder, showing as many as four or five elements in a radially disposed row, while the maple rarely shows more than three in a group. The medullary rays are not so straight in the box elder, hence the radial section does not show such large plates of "silver grain" as in the maple.

Fig. 39 shows a bit of the cross-section of box elder wood highly magnified. The tracheae are elliptical or oval in section, with the longer axis radially disposed. They range in size from 30 μ to 65 μ, with an average size of 40 μ×55 μ. The individual cells of which the tracheae are composed are 150–200 μ long, with their end walls obliquely disposed at an angle of about 45°, the dip in almost every case being radial, so that the end wall seems to be quite transverse as seen in tangential section (fig. 31). The perforation through the end wall is about one-half the size of the end plate, and elliptical in shape. The tracheal walls are marked off in a regular hexagonal pattern, each area of which is about 5 μ across, with a simple pit 0.3 μ×1.5 μ transversely disposed at the center. Where tracheae lie in contact with medullary rays, the pits are circular and 1.5–2.5 μ in diameter. Some smaller tracheae show occasional traces of scalariform and even spiral thickening of the walls. In the acute angle with the oblique end wall, there is sometimes a considerable area of the tracheal wall in which the thickness is uniform and unbroken by pits. In these regions quantities of tannin may be stored.

The tracheids of box elder are of three fairly distinct sorts. (1) The thin-walled summer tracheids are 12–15 μ in diameter, with walls only 0.5–0.8 μ thick. These occur in largest proportion near the beginning of the season's growth, but they are also to be found in small numbers even bordering upon the zone of the thick-walled autumn cells. (2) The thick-walled summer tracheids are 8–10 μ in diameter, and their walls are 1.5–2.5 μ thick. These occur in small groups at the beginning of the annual ring, the groups becoming larger and more numerous as the season's growth progresses. The two kinds of summer tracheids are commonly grouped in such a way as to give a distinctly marbled appearance to the cross-section. All of these cells are angular and very irregular in shape. The majority of them are 400–600 μ in length, and they are firmly interlocked at the ends. (3) The autumn tracheids constitute a dense zone 3–6 cells thick at the close of the season's growth. These cells are much flattened, measuring 10–15 μ tangentially and 5–7 μ radially. The walls are 2 μ or more in thickness and more strongly lignified than other parts of the wood. This zone of autumn tracheids is frequently divided into two parts by the interpolation of a few thick-walled summer tracheids. All tracheids show a few small circular pits in their walls at points of contact with medullary rays, while elsewhere their pits are very rare. Faint oblique striae are occasionally found in the walls of the thicker-walled sorts.

Wood parenchyma cells in the mature parts of box elder are very few, small, short, and thin-walled. They are usually found bordering upon the larger tracheae. Very rarely they become crystallogenous. The medullary rays are 1–3-seriate, about 100–120 μ apart, and slightly wavy as seen in cross-section of the wood. In radial and tangential sections the medullary rays show a breadth of about 200–500 μ, and a thickness of about 20 μ. The ray cells are of two fairly distinct kinds (figs. 34, 36). (1) The ray body cells are nearly cylindrical, 7–10 μ in diameter, with walls 2–2.5 μ thick. Their length is from 25 μ to 40 μ, except in the region of the autumn growth, where the length hardly exceeds the diameter, and where the walls are slightly thicker. The end walls are usually only slightly oblique, with very many minute simple pits. The pits communicating with the tracheae are large and numerous, while those connecting with tracheids are small and few. (2) The ray marginal cells form usually a single, sometimes a double, row on each edge of the ray. These are a little larger than the ray body cells, with somewhat thinner walls. They are triangular in section, and when seen in radial sections they show marked irregularity in form along the free border (fig. 36). The pits are larger and more numerous than in the body cells. Much protoplasm and large nuclei are usually to be seen in the ray body cells, while the marginal cells are usually almost empty.

Where injuries have been inflicted, the wood of box elder shows traumatic tissue made up of thin-walled, unlignified cells containing a very little tannin.

As would be expected from the comparison of figs. 27 and 30, the density of box elder wood is considerably less than that of the maples. The average for box elder wood is 27 pounds per cubic foot, while the maples range from 32 to 43 pounds per cubic foot. In color the wood of box elder is a pale cream or white. Its rather coarse and uneven texture makes it unfit for the more exacting uses to which maple wood is commonly put.

The wood of *A. saccharinum* is shown in figs. 26, 27, 28, and 38. Here the tracheae are nearly circular in section, except where two or three are crowded together. The diameter is 20–40 μ, and the walls are 0.7–0.8 μ thick. In the older wood the tracheae often contain tannin plugs 250–300 μ in length. The oblique end walls have in most cases a tangential dip of 40–60°. The pit areas are hexagonal and 5–6 μ in diameter. The transverse pits are about 1 $\mu \times 2 \mu$. The thickenings in the walls of the smaller tracheae are sometimes scalariform, but *not* spiral. The tracheids are of two sorts, both rectangular in section in a large proportion of cases. (1) The summer tracheids are about 8–12 μ across, with walls 1–1.5 μ thick, more highly lignified in the neighborhood of the tracheae. (2) The autumn tracheids appear as 1–3 rows of much flattened cells, 4–5 $\mu \times 10 \mu$, with walls 1.5–2 μ thick. There is often a very gradual transition from summer to autumn types of cells. The tracheids are 250–300 μ long. Some wood parenchyma cells occur near the tracheae, but they do not contain either resin or crystals.

The medullary rays are 1–3-seriate, 125–150 μ apart, 200–500 μ broad, and 20–30 μ thick. The body cells are cylindrical, 6–10 μ in diameter and 30–60 μ long, with walls 0.7 μ thick. The marginal cells are a little larger, triangular in section, and quite straight on the outer margin, as in the case of other true maples (figs. 35, 37). The pits are circular, large, and very numerous at points of contact with the tracheae. All ray cells contain much protoplasm and some starch. The end walls as seen in radial section are but slightly oblique, while in the transverse section they stand at an angle of 20–30°. Large parenchymatous masses appear at intervals, connected with the medullary rays.

In *A. platanoides* the tracheae are nearly round in transverse section, occurring in irregular groups. The end walls have a tangential dip of 30–40°. The smaller vessels show well marked spiral thickenings in their walls. The tracheids are of only one general sort, with a very gradual increase in thickness of walls and in lignification through the year's growth. All are very irregular in shape. Some are considerably distended and show numerous pits. Tannin is found in these larger cells. There are but few wood parenchyma cells, and these do not contain crystals. Tracheae in the older parts of the wood contain much tannin and some tyloses. The medullary rays do not differ essentially from those of *A. saccharinum*, except that the cells are much shorter at the close of the season's growth, and elsewhere an occasional cell is shorter, thick-walled, and filled with tannin.

In *A. saccharum* the end walls of tracheal cells are about 45° oblique, but with no definite direction of dip. The smaller tracheae show scalariform and imperfect spiral markings. Tracheids are of three kinds, quite similar to those of box elder. Crystallogenous wood parenchyma cells are numerous, especially along the sides of the medullary rays. The ray marginal cells are very irregular in shape, and show a marked tendency to overlap each other.

In *A. rubrum* the end walls of the tracheal cells have a dip of 30–60°, chiefly in the tangential direction. The smaller vessels show scalariform but not spiral markings. There are occasional tannin plugs and diaphragms in the tracheae of the older wood. Tracheids are of two types. The autumn tracheids are flattened to a greater extent than in other species, measuring 10–14 μ by only 3–4 μ in cross-section. The wall is 1.5 μ thick except near the edges of the flat cells, where it is 2 μ or more. Many older tracheids contain crystals and tannin, and small simple pits are common in the walls. The medullary ray cells are often hexagonal in tangential view, and the walls are unusually thick. The rays are frequently much broader than in other species. The marginal cells are larger and quite irregular. They are much shorter at close of the season's growth, and often erect on the edge of the ray. The most striking feature of this species is found in the much greater number and larger size of pits in all kinds of elements than in other species of maple.

Further details in regard to size of elements in the wood of the various species studied may be found in the table of measurements on p. 177.

Anatomy of the leaf

It has already been stated that the leaf of box elder is thicker and of softer texture than are the leaves of the true maples. The principal features of the minute structure are indicated in fig. 32.

Palisade tissue is developed to an unusual degree, there being at least two well defined rows of these cells, and often as many as four, in which case there is scarcely any spongiophyll and the air spaces are small and few. Where the spongy layer is prominent, there are groups of collecting cells at the lower ends of the deepest palisade cells. Protoplasm is abundant in all palisade and sponge cells, where chlorophyll is also present in large amounts. Crystallogenous cells are found in small numbers. The upper epidermis is made up of medium-sized, lenticular, empty cells, which are regular and even in arrangement, and covered with a moderately thick cuticle. The lower epidermis is composed of cells much less uniform in size and shape, and in consequence the lower surface of the leaf is not so smooth as the upper. A few small hairs may be found widely scattered over the lower surface of the older leaves; hairs are quite numerous on younger leaves. The stomata are small, but very numerous, with the guard cells set flush with the lower surface. The midrib of the leaflet of box elder is very similar to that of *A. rubrum* (fig. 18), except that the crest of spongy tissue on top is even more prominent.

In all of the maple leaves examined, there was found but one rank of palisade cells, and these formed not more, and usually much less, than half the thickness of the lamina (fig. 18). No well defined zone of collecting cells was observed. The spongiophyll contains many good sized air spaces, except in *A. platanoides*. The epidermal cells of both surfaces are quite varied in size, and the cuticle is thin. Stomata are comparatively few and somewhat depressed from the surface. The midrib crest is present in all forms, but not so large as in box elder. Hairs are short and few on all types but *A. platanoides*, where they are quite numerous and long. A section of *A. saccharinum* leaf is shown in fig. 33.

The petiole of box elder presents some interesting structural features (fig. 9). If we follow the three large leaf traces a little way up the petiole from their emergence from the stem, they are found to break up into a considerable number of fibrovascular strands arranged in an interrupted ring around a large medulla. A little farther out, not more than one-fourth of the way to the first pair of leaflets, there will usually appear from 1 to 4 or 5 medullary fibrovascular strands, which become larger out to the first pair of leaflets. Beyond that point these strands are smaller, and they may be fewer. These medullary strands are larger and more numerous in petioles of leaves having the larger numbers of leaflets. In these cases the strands are often typically amphivasal, but with the greater part of the xylem directed upward. Large cells and ducts appear in the cortex, similar to those found in the cortex of the root. Neither *A. saccharum* nor *A. platanoides* (fig. 10) develops medullary strands in the petioles. In *A. rubrum* (fig. 8) there is a single small centrivasal strand, conspicuous for its dense and tanniniferous phloem. In *A. saccharinum* there are a few very small medullary strands clustered near a sclerotic rib that projects into the upper side of the medulla. In neither of these cases, however, is there any indication of a true amphivasal condition. The petiole of box elder is larger and less compact than that of the true maples. Sclerotic tissue is almost entirely wanting, and the same is true of crystallogenous and tanniniferous cells. All of the maples possess these three sorts of cells in greater or less amount. The petiole of *A. rubrum* is particularly dense (fig. 8).

Anatomy of reproductive axis and fruit

The reproductive axis of box elder is characteristically compressed, so that the cross-section is a broad ellipse, with axes about in the ratio of 3:4 (fig. 5). The surface is ribbed and the cuticle is very thick. The pith is composed of cells of very unequal size, some of them quite large. The xylem ring is interrupted by 10–15 one or two-seriate medullary rays. The hard bast is prominently developed in a thick continuous zone which is crowded close upon the phloem. All cell walls are comparatively thick.

In *A. platanoides* (fig. 4), which is fairly typical of the maples, the reproductive axis is quite cylindrical, smooth, and covered with a thin cuticle. The pith cells are uniformly rather small. The xylem ring is interrupted by 5–8 two to six-seriate rays. The hard bast zone is but slightly developed, narrow, widely interrupted, and remote from the young phloem. Compared with the vegetative stems, the reproductive axis of box elder and the maples shows an almost complete reversal of structural characteristics, but with far more conspicuous differences.

Fig. 21 shows a section through the fruit (samara) of box elder at about the mid-level of the embryo. The walls of the seed vessel are very thick throughout, with a dense fibrous sclerotic lining of remarkable thickness. The fibrovascular strands are not very numerous, but some of them are quite large, with dense, centrifugally massed pericycle. There is a subepidermal sclerotic zone of usually one layer of large thick-walled cells. The embryo is simply and symmetrically folded, and surrounded by a moderately thick, tanniniferous coat.

Figs. 20 and 22 show sections of the fruit of *A. platanoides*. The wall is very thick at the base, but much thinner around the embryo. There is a fibrous sclerenchyma lining only near the base, and it is not thick or dense even here. Fibrovascular strands are numerous, but all are small. The subepidermal sclerotic zone is composed of small, thin-walled cells. The embryo is very irregularly folded, and covered with a thick, dense, tanniniferous coat.

The box elder fruit is clearly better fitted to withstand unfavorable weather conditions than is the fruit of the maple.

Geological record of box elder

The *Acer* group apparently made its first appearance in the Upper Cretaceous, and became widespread and diversified in species during the Eocene, in which fossil remains of various maples are abundant. However, there is recorded only a single instance of the mention of *Acer Negundo* in a fossil state, and that in the Miocene at Oeningen in Baden (Neues Jahrb. 1835. p. 55). But since this record has not been referred to by any recent authority, it may be set aside as of very doubtful value. Fossil leaves of the *Negundo*-like type are of rather frequent occurrence as far back as the Upper Cretaceous. LESQUEREAUX in 1868 founded the genus *Negundoides* for a single species from the Cretaceous (Dakota Group) of Nebraska, but PAX, in his revision of *Acer*, reduced this genus to *Negundo* (Bot. Jahrb. **6**:346. 1885). Under the genus *Negundo* the following fossil species have been described: EOCENE, *N. europaeum* Heer (Switzerland and Oeningen in Baden), *N.*

decurrens Lesq. (Colorado), *N. triloba* Newberry (Ft. Union Beds, North Dakota); OLIGOCENE, *N. bohemica* Menzel (Bohemia); MIOCENE, *N. trifoliata* Braun (Oeningen in Baden), *A. Negundo* (from Oeningen, 1835; doubtful). To these may be added the apparent box elder described by KNOWLTON, under the name of *Rulac crataegifolium*, from the Miocene of the John Day Basin, Oregon (Bull. U.S. Geol. Surv. no. 204. p. 77. *pl. 16. fig. 7*).

Since the Glacial Period the *Negundo* type has been abundant and varied throughout all of the morainal regions. The remarkable elasticity of the type under shifting stress of environment doubtless accounts in large measure for its unusual success.

Theoretical considerations

As a result of the studies and observations outlined in this paper, the writer is of the opinion that the box elder, in its present highly specialized form, is a product of the Glacial Period. The evidence may be stated concisely as follows:

1. *Negundo* characters were but slightly developed before the Pleistocene or Glacial Period. They have been widespread since that time. *Negundo* occurs in greatest abundance in regions of the richest glacial drift, especially upon and below the great terminal moraines.

2. *Negundo* characters were apparently developed rapidly, and partially fixed, through exposure to the inclement conditions along the margins of the great continental ice sheet.

3. *Negundo* was apparently a primitive variant from the ancestral *Acer* stock, possessing peculiarities especially adapted to glacial conditions. These features were greatly emphasized by the glacial experience of the species. The impetus gained from glacial influences is not yet lost. *Negundo* is highly variable, yet irretrievably separated from the true maples. The nearest points of correspondence are found in *A. pennsylvanica*, *A. spicatum*, and *A. platanoides*.

4. Characters of *Negundo* that would fit it for glacial environment are as follows: (*a*) leaf morphology and anatomy; maximum utilization of light; (*b*) medullary strands in petiole; great capacity for transportation; (*c*) extended insertion of leaf trace into stele;

(*d*) color of twigs; energy absorption; protection; (*e*) indeterminate growth; maximum growing season; (*f*) food storage capacity; amyliferous tissue; (*g*) high vitality of lateral buds; (*h*) vegetative activity of shoots; quick response to warmth and light; rhizogeny; (*i*) medullary rays; marginal cells; extension into bark; (*j*) large and numerous pits in wood elements; (*k*) bark; thick, tough, elastic, persistent; (*l*) unobstructed conduction in roots; (*m*) great extent of root system; (*n*) large number of seeds; (*o*) anemophily; (*p*) extreme protection of embryo; thick, resistant seed coats; (*q*) food storage in embryo; (*r*) fruit long persistent on the tree.

Summary and conclusions

1. *Negundo aceroides* does not appear as an authentic species in the geological record before the Glacial Period.

2. The fundamental *Negundo* characters made their appearance as early as the Upper Cretaceous, but only as minor variations from the *Acer* type.

3. In structure of leaf, efficiency of transporting tissue, capacity of storage organs, and in maximum utilization of light, heat, and growing season, *Negundo* became peculiarly adapted to the rigors of a glacial environment.

4. The impetus acquired by *Negundo* during the strenuous period of its adaptation to glacial conditions is still manifest in the pronounced inconstancy of the *Negundo* type. However, there seems to be no true reversion to the pre-glacial ancestral forms.

5. In practically every particular, except the morphology of the fruit, *Negundo* is now essentially different from the true maples.

6. Upon purely anatomical grounds, it appears that *Negundo* possesses characteristics of generic rank, and while the box elder is undoubtedly a descendant from the ancestral *Acer* stock, it has now reached a stage of differential development that may fairly exclude it from the group of true maples. Thus there seems to be ample justification for the name "*Negundo aceroides* Moench. 1794."

In conclusion, I wish to express my thanks to Professor F. H. KNOWLTON for facts in regard to the geological record of the box

elder; and to Professor WILLIAM TRELEASE for valuable suggestions and for his lively and encouraging interest in the progress of this work.

WAUKESHA, WIS.

EXPLANATION OF PLATES V–X

FIG. 1.—Photograph showing the commoner types of box elder leaves; $\times\frac{1}{5}$.

FIG. 2.—Trunk surface of box elder; $\times\frac{1}{7}$.

FIG. 3.—Trunk surface of *Acer saccharinum;* $\times\frac{1}{6}$.

FIG. 4.—Transverse section of the reproductive axis of *Acer platanoides;* ×20.

FIG. 5.—Transverse section of the reproductive axis of box elder; ×20.

FIG. 6.—Transverse section of young root of *A. rubrum;* ×20.

FIG. 7.—Transverse section of young root of box elder; ×20.

FIG. 8.—Transverse section of petiole of *A. rubrum;* ×20.

FIG. 9.—Transverse section of petiole of box elder; ×20.

FIG. 10.—Tranverse section of petiole of *A. platanoides;* ×20.

FIG. 11.—Radial section of the bark and outer wood of an older root of *A. rubrum;* ×20.

FIG. 12.—Transverse section of the bark and outer wood of an older root of *A. rubrum;* ×20.

FIG. 13.—Transverse section of the wood and bark of a 10-year stem of box elder; ×20.

FIG. 14.—Transverse section of the wood and bark of a 12-year stem of *A. platanoides;* ×20.

FIG. 15.—Transverse section of the wood and bark of an 8-year stem of *A. saccharum;* ×20.

FIG. 16.—Transverse section of the wood and bark of a 20-year stem of *A. rubrum;* ×20.

FIG. 17.—Transverse section of a vigorous 1-year stem of *A. saccharinum;* ×15.

FIG. 18.—Transverse section of the midrib of the leaf of *A. rubrum;* ×25.

FIG. 19.—Transverse section of a vigorous 1-year stem of box elder; ×10.

FIG. 20.—Transverse section of a seed of *A. platanoides;* ×8.

FIG. 21.—Transverse section of a seed of box elder; ×15.

FIG. 22.—Tranverse section through the base of the samara of *A. platanoides;* ×8.

FIG. 23.—Tangential section of the bark of *A. rubrum;* ×20.

FIG 24.—Tangential section of the bark of box elder; ×20.

FIG. 25.—Radial section of wood and bark of box elder; ×20.

FIG. 26.—Radial section of wood of *A. saccharinum;* ×20.

FIG. 27.—Transverse section of wood of *A. saccharinum;* ×20.

FIG. 28.—Tangential section of wood of *A. saccharinum;* ×20.

FIG. 29.—Radial section of wood of box elder; ×20.

FIG. 30.—Transverse section of wood of box elder; ×20.

FIG. 31.—Tangential section of wood of box elder; ×20.

FIG. 32.—Transverse section of leaf of box elder; ×500.

FIG. 33.—Transverse section of leaf of *A. saccharinum;* ×500.

FIG. 34.—Tangential section, medullary ray of box elder; ×500.

FIG. 35.—Tangential section, medullary ray of *A. platanoides;* ×500.

FIG. 36.—Radial section, medullary ray of box elder; ×500.

FIG. 37.—Radial section, medullary ray of *A. rubrum;* ×500.

FIG. 38.—Transverse section of wood of *A. saccharinum;* ×500.

FIG. 39.—Transverse section of wood of box elder; ×500.

FIG. 40.—Transverse section through the amyliferous zone of the medulla of box elder; ×500.

FIG. 41.—Transverse section through the amyliferous zone of the medulla of *A. saccharinum;* ×500.